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THE BOTANICAL REVIEW

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DEVELOPMENT AND STRUCTURE OF THE PHLOEM TISSUE. II [1]

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INTRODUCTION

The new literature on the development and structure of the phloem is not voluminous but it has caused some important changes in the terminology and concepts regarding this tissue. Some investigations have clarified details in the ontogeny of the phloem and have contributed toward the understanding of its seasonal changes. The phylogenetic aspects of the sieve-tube structure in the monocotyledons have been thoroughly investigated and, concomitantly, some advance made toward the establishment of a uniform terminology regarding the conducting elements. The controversial topic of the structure of the sieve element as related to its function was subjected to experimental studies and was much discussed. As a result, comprehension of the essential characteristics of the protoplast of a sieve element has been deepened.

The present review has a three-fold purpose: to sum up the work that has been done on the phloem tissue during the past ten years; to stabilize, as far as possible, the terms used with reference to the tissue and its components; and to bring up to date the concepts on the relation between the structure of the sieve element and its function. It has a somewhat different topical arrangement than the previous review, and the topics to which no new information has been added are entirely omitted. Such topics are: historical data; ontogentic transformations of the sieve element; characteristics of the parenchymatous elements of the phloem; interconnection of phloem cells; and the phloem in vein endings of leaves.[2]

[1] Supplement to article in The Botanical Review **5**: 373-432. 1939.

[2] There is, however, a report (86*a*) on the quantitative aspect of phloem distribution in the veins of leaves. According to the investigators, six dicotyledonous species contained only parenchyma in the phloem of minor veins, and these veins composed 95 per cent of the total vein length of the blade.

The studies on the relation between the function and structure of the sieve element are given special attention. By considering the methods employed by the investigators, as well as their conclusions, a critical evaluation of the various concepts on the nature of the sieve-element protoplast is attempted.

THE CONDUCTING ELEMENTS

CLASSIFICATION. Since the appearance of the first review on the phloem tissue in this journal (33), a practical terminology has been proposed by Cheadle and Whitford (15) for the designation of the characteristic conducting elements of the phloem. According to this terminology, the elements in question bear "sieve areas" on their walls, that is, pit-like[3] recesses where pores with connecting strands are grouped. The sieve areas are variously distributed on the wall and may be unlike on different parts of them. A wall or part of a wall bearing one or more highly specialized sieve areas, that is, areas with particularly conspicuous connecting strands, is referred to as "sieve plate". A parallel term for the xylem is "perforation plate", denoting the area of the vessel wall which is involved in the coalescence of two members of a vessel (18). If the sieve plate shows a uniform distribution of pores (one sieve area), it is called a "simple sieve plate"; if the pores are in clusters arranged in scalariform, reticulate or any other manner (several sieve areas), the sieve plate is "compound". Most commonly it is the end (or terminal) wall, transverse or inclined, that is differentiated as a sieve plate, but such structures may be found on longitudinal (or lateral) walls as well.

Conducting elements having sieve plates are usually disposed in long series end to end. These series are the "sieve tubes". One unit of such a series is a "sieve-tube member" (15), or a "sieve-tube element". Thus a sieve-tube member may be characterized as a cell "in which certain sieve areas are more highly specialized than

[3] According to the Committee on Nomenclature (18), "pit" designates a recess in a secondary wall only, and "primary pit field" a thin area of the primary wall and intercellular material. Such a strict distinction between the terms "primary pit field" and "pit" requires an equally accurate recognition of primary and secondary walls. A precise diagnosis of the nature of walls is often beyond the scope of an anatomical study, and then the investigator is left without a term for the thin areas in the walls. As in the previous review (33), the present writer again uses "pit" to identify a recess in either a primary or a secondary wall.

others, the former being largely localized on end walls to form the sieve plates" (15). If "the sieve areas of all walls are of the same degree of specialization" and no wall parts can be conveniently distinguished from others as sieve plates, the conducting element constitutes a "sieve cell" (15). The sieve cells are commonly elongated elements with tapering ends and are not arranged in longitudinal series like the sieve-tube members. Cheadle and Whitford (15) include in the definitions of the conducting elements the absence of nuclei and the deposition of callose around each connecting strand of a sieve area.

It is of interest to recall at this point that Hartig (58), who discovered the sieve element, was aware of the difference between sieve cells and sieve tubes, and used the term "Siebfaser" to designate the former.

The terminology just considered does not suggest a name that would include both the sieve-tube members and the sieve cells. In this review the two types of cells will be united under the term "sieve element" which was recently adopted by Eames and MacDaniels (30, p. 103). It is admittedly not an entirely satisfactory term because it can be confused with "sieve-tube element", but it has the advantage of utilizing a well known word, "sieve", which is rather universally associated with the conducting elements of the phloem, and it is not a new term.

The terminology given above parallels that which is used with reference to the conducting elements in the xylem. While the phloem has "sieve elements", which may be segregated into "sieve cells" and "sieve-tube members" (or "sieve-tube elements"), in the xylem there are "tracheary elements" (50) of two types, the "tracheids" and the "vessel members" (or "vessel elements"). Whereas sieve-tube members are combined into "sieve tubes", vessel members form "vessels". In both groups of terms the degree of specialization of the characteristic wall structures determines the final classification. The higher degree of specialization in the sieve elements is reportedly expressed in the enlargement of the connecting strands and, consequently, also in the increase in diameter of pores and of the callose cylinders encasing the strands. In the tracheary elements specialization has led to the removal of parts of wall and the establishment of direct continuity between the individual cells. The sieve cell is regarded as more primitive

than the sieve-tube element; similarly the tracheid is interpreted as a more ancient type of cell than the vessel element.

Sieve-tube members are usually associated with specialized parenchyma cells, the "companion cells", which are ontogenetically related to the sieve-tube members. Sieve cells of gymnosperms and still lower vascular plants are not known to be accompanied by similar cells, except that in the gymnosperms the "albuminous cells" of the rays appear to be physiologically associated with the sieve cells. According to Barghoorn (*7a*), "albuminous cell" should be abandoned and replaced by "erect phloem ray cell" because the former term implies a protoplasmic peculiarity as yet unsubstantiated. Barghoorn thinks the dense staining of the albuminous cells is related to their narrow diameters and to the resulting retention of whole protoplasts in sections, in which larger cells, in contrast, are cut open and lose part of their cytoplasm. He also stresses that, contrary to a common concept, the albuminous cells do contain starch. As was pointed out in the previous review (33, p. 410), the albuminous cells have been reported occurring not only in the rays of gymnosperms, but also in the vertical system, where, except for the appearance of their protoplasts, they resemble the phloem parenchyma cells. Furthermore the presence of starch during certain times in the life of the albuminous cells was recognized by their discoverer, Strasburger. Although the term " albuminous cell" is unsatisfactory, the abandonment of the concept is not justified by the available information.

SIEVE AREAS. The sieve areas are comparable to pits in living cells in that they constitute thin places in the wall, in which the strands connecting the protoplasts of the superposed or adjacent cells are aggregated. Since the exact nature of the connecting strands, that is, whether they are entirely similar to plasmodesmata or not, is not yet known (see 33 and part of this review concerned with the relation between the structure and function of the sieve element), the present reviewer prefers the term "connecting strands" for the designation of these structures.

Sometimes a sieve area is clearly circumscribed and is uniformly thin throughout its extent; or it appears to be broken up into smaller units separated from each other by slightly thicker wall portions, not so thick, however, as the unpitted parts of the wall.

Even single strands may be surrounded by thickened wall portions (see example in 44). The various patterns assumed by the sieve areas are, of course, related to the method of cellulose deposition in primary walls. As is well known, the deposition of fibrils of cellulose in such walls is not uniform throughout, and some fibrils may subdivide the original primordial pit area into smaller ones, thus creating a field of pits, which all together are recessed within the unpitted part of the wall (e.g., 7, 97). The question then, whether a whole sieve area, or part of it, or one connecting strand, corresponds to a pit (see 33), has no simple answer. Varied situations occur and it is possible that in plants with particularly large strands an entire pit with several plasmodesmata is converted into one connecting strand. Still other variations are possible, such, for example, as the inclusion of several connecting strands in one callus cylinder—a pattern reportedly characteristic of gymnosperms (33).

The combination of all pit-like wall structures of the sieve elements under one term, "sieve area", as proposed by Cheadle and Whitford (15), is to be desired, firstly because the various sieve areas appear to be fundamentally similar in their make up, and, secondly, because sieve areas of distinctly different degrees of differentiation may be connected by transitional structures in one and the same cell (33, 44).

The view on the spatial relation of callose and cellulose in the sieve areas has remained largely unchanged in the works on phloem. Each connecting strand is at first enclosed in a callus cylinder, but later large masses of callose are deposited on the sieve area, the connecting strands becoming longer and thinner in the process. If the deposition of the callose is associated with a complete cessation of function of the sieve element, the accumulations on the sieve plate are called "definitive callus"; the callus masses which occur during a temporary break in activity, as in *Vitis*, may be termed "provisional" or "dormancy callus" (33, 44).

The implausible assumption that the callose is derived from the sieve-tube slime has again appeared in the phloem literature (95).

THICKENING OF LATERAL WALLS. The occurrence of thick, apparently hydrated walls in differentiating and mature sieve elements has been observed in many plants of different taxonomic groups (33). These walls are commonly designated as "nacré",

a term taken from the French literature (33). No satisfactory substitute term has been as yet proposed, principally because information on the nature of this wall is still rather fragmentary.

It has been recorded that the nacré thickening is transitory, that it loses water and becomes thinner as the sieve element ages (33). This reduction in thickness is not necessarily a constant character. Thus, according to Sterling (110), the nacré thickening of protophloem cells in *Sequoia* persists until the cells are obliterated.

Schneider (100) recently confirmed the cellulose nature of the nacré thickening, using peach and cherry phloem. Crafts (24, 25) and Sterling (110), studying gymnosperms, found it to be doubly refractive.

Some plants appear to lack the special thickening of sieve-element walls. For example, it is not characteristic of *Vitis* sieve tubes, at least not of those in the secondary phloem (44).

SIEVE ELEMENTS IN DIFFERENT GROUPS OF PLANTS

The revised terminology regarding the conducting elements of the phloem calls for a reexamination of these structures in the different groups of plants, especially in those bearing no seeds. Although descriptions of sieve elements in the lower vascular plants have been given, they were written mostly by authors who did not have in mind the distinction between sieve cells and sieve-tube elements. Furthermore, the evolutionary trends in the structure of the phloem and its elements are not yet adequately known in the vascular plants in general. The following attempt at classifying the sieve elements in different groups of plants is therefore entirely tentative.

DICOTYLEDONS. The angiosperms generally have sieve tubes in both the primary and the secondary phloem. In dicotyledons the primary sieve-tube elements apparently vary less in structure than the secondary. The former usually have transverse or slightly inclined end walls bearing simple sieve plates. The secondary sieve-tube elements range from types more or less resembling the sieve cells of gymnosperms, as in *Pyrus, Sambucus* (74) and *Sorbus* (62), to those with transverse end walls bearing highly differentiated simple sieve plates (e.g., herbaceous species, *Robinia*). On the basis of the very meager comparative data on the phloem of dicotyledons (60–62, 74, 83), the concept has been

formulated that the phylogenetic specialization of the sieve elements in this group of plants involved a shortening of individual cells; a decrease in inclination of end walls; a decrease in elaboration of sieve areas on longitudinal walls; and an increase in the size of pores in the sieve areas of the sieve plates. This concept obviously suggests a parallelism between the evolution of the sieve elements and that of the tracheary elements in the xylem.

MONOCOTYLEDONS. The thorough survey of the metaphloem in monocotyledons by Cheadle and associate (14–16) strengthens the concept of evolution of the sieve element just outlined for the dicotyledons. In 219 species in 158 genera of 33 families of monocotyledons, only sieve tubes were found in the metaphloem. The trends in the specialization of these elements may be summed up as follows: progressive localization of highly specialized sieve areas on the end walls; gradual change from very oblique to transversely placed end walls; gradual change from compound to simple sieve plate; and progressive decrease in conspicuousness of the sieve areas on the side walls.

Authors (14, 15) generally found the most highly evolved sieve tubes in leaves, in inflorescence axes, corms and rhizomes; the less highly specialized ones in the roots. The sieve tubes of the aerial stems occupy an intermediate position. Such course of evolution in the phloem of the plant as a whole is the reverse of that in the xylem; the vessels specialize first in the roots and then upwardly throughout the shoot (16).

The degree of specialization of the sieve elements, as expressed in the position of the end wall, is correlated with the specialization of the plant or organ as a whole (15). The sieve elements in the families Palmae, Pandanaceae, Dioscoreaceae, Smilacaceae, and in some of the Liliaceae have inclined end walls in stems and roots. Similar sieve-tube end walls occur in the roots of the Agavaceae, Zingiberaceae, and in many Liliaceae. All these families or genera are perennial and commonly woody in nature. The sieve elements in plants with corms and bulbs (e.g., Amaryllidaceae), in hydrophytes, and apparently in most of the sedges and grasses have transverse end walls. The same type of wall is characteristic also of the annuals, including annual roots, and of the parts of perennial plants that are annual in nature.

With regard to the phloem of the monocotyledons, the struc-

tures described by Mason (77) in *Dioscorea* have been given renewed consideration. According to Mason, at each node of this plant glomeruli composed of peculiar parenchyma cells intervene between the sieve-tube strands of the superposed internodes. Roeckl (91), however, found evidence that these glomeruli might be composed of sieve elements and that therefore the phloem does not appear to be interrupted at the nodes by non-typical phloem tissue.

GYMNOSPERMS. The secondary sieve elements of gymnosperms are sieve cells. They are elongated and tapering in shape and lack sieve plates. The primary sieve elements in this group of plants are probably sieve cells also (24, 25, 56, 110, 111), although in the leaves of the conifers these elements are described as having nearly transverse end walls with sieve areas on the latter only. The nature of the very first phloem elements seems to be uncertain. They show no distinct sieve areas and may contain dense cytoplasm (56, 110, 111). Perhaps these elements are of the type described by Chauveaud (see 33) as "precursory phloem" which he found below the cotyledons in gymnosperm seedlings. Gunckel and Wetmore (56), who recognized such imperfectly developed phloem elements in the protophloem of the shoot system of *Ginkgo*, prefer to classify them as "sieve cells" because they are connected by transitional types of cells with the later-formed primary sieve cells. Bouvrain (11*a*, *b*) reports having found precursory phloem in the seedling roots of certain dicotyledons, but furnishes no satisfactory proof that the structures in question are not ordinary protophloem sieve tubes.

LOWER VASCULAR PLANTS. The sieve elements of the non-seed-bearing vascular plants would probably fall mostly into the class of sieve cells (see 33). It is of interest that Russow (93) distinguished between sieve cells (which he called "Siebröhren") and sieve tubes ("Siebgefässe") in these plants and stated that the various vascular cryptogams have mostly long spindle-shaped sieve elements, except *Equisetum* and the Ophioglossaceae in which these elements are prismatic with horizontal or somewhat inclined end walls, and occur in continuous files. Dippel (29), who apparently discovered the sieve elements in the cryptogams, also noted the horizontal end walls in the phloem elements of

Equisetum. It is possible, of course, that despite their shape these sieve elements have no sieve plates in the sense of Cheadle and Whitford (15) and should be called "sieve cells", as was done by Golub and Wetmore.

According to the somewhat detailed study and drawings of West and Takeda (124), the sieve elements of *Isoetes* resemble primary sieve-tube elements of the dicotyledons in their shape. They have transverse or somewhat inclined end walls. Sieve areas occur on all walls, but on the end walls the callus masses develop more prominently than on the lateral walls.

These few references to the phloem of the lower vascular plants should suffice to illustrate the fragmentary nature of the data about the sieve elements in these groups.

ALGAE. Since the sieve elements of Laminariaceae are so similar to those of herbaceous angiosperms, they probably should be called "sieve-tube elements". A new study of these structures by Smith (109) did not contribute toward their proper classification. In fact, disagreeing with previous workers (see 33), Smith identified sieve elements only in *Nereocystis*. He used an unusual method for identifying sieve tubes: instead of looking for connecting strands and the associated callus, he strived to see holes in the sieve plates, a rather problematical undertaking when the connecting strands, and consequently also the pores, are as fine as those in the Laminariaceae. Smith also reports that nuclei are present in the sieve tubes of *Nereocystis*.

CONCLUSION. Thus the presently available information on the types of sieve elements in different groups of plants suggests that sieve tubes are characteristic of the primary and secondary phloem of angiosperms and also occur in certain brown algae; that gymnosperms and the non-seed-bearing vascular plants typically possess sieve cells; and that the lower angiosperms have sieve elements which resemble sieve cells or are perhaps transitional between sieve cells and sieve-tube elements.

THE PROTOPLAST OF THE SIEVE ELEMENT

THE ENUCLEATE CONDITION. The protoplast of the sieve element has been intensively studied by investigators interested in the problem of translocation of organic solutes. Its cytoplasm has

been variously interpreted as showing properties of normal living substance or as being denatured and having lost its property of differential permeability. These concepts are examined in detail in the part of this review dealing with the relation between structure and function of the sieve element.

The enucleate condition of the sieve-element protoplast is a well known characteristic (see 33) and has recently been confirmed for a large number of angiosperms not previously investigated from this viewpoint (95). The absence of a discrete nucleus from a fully differentiated sieve element raises the question of appropriateness of the name "protoplast" for the contents of such an element. "Cytoplasm" alone does not properly describe these contents because in a certain sense they are organized as a vital unit, somewhat like a protoplast: a parietal layer of cytoplasm encloses a vacuole (often rich in colloidal matter, the slime) and this unit is able to perform some vital functions after loss of the nucleus. The present reviewer favors the continued application of the term "protoplast" with reference to this enucleate unit of living matter with its non-living inclusions. The term "cytoplast", which is present in biological literature, seems to be less appropriate because it denotes the cytoplasmic part of a cell as distinguished from the nucleus and does not appear to imply enucleate condition.

A discussion of the sieve-element protoplast usually brings up the disputed point about the stage of development of this protoplast that coincides with the functioning state of the element. The majority of workers consider that the functioning period of the element begins after disintegration of the nucleus and dispersal of the precursors of the slime, the "slime bodies". At this stage the connecting strands are most conspicuous because of their thickness and density of staining, and are associated with only small amounts of callose. The evidence that such elements are in a functioning state is, of course, indirect. The developmental stages are passed rather rapidly, and the sieve elements are without nuclei during the longest time of their existence as intact cells.

The occurrence of dormancy and reactivation in grape phloem offers a unique opportunity of testing the anatomist's notion of a functioning sieve tube (44). The phloem of *Vitis* functions for more than one season and passes, in the aerial parts of the plant, through a period of dormancy during the winter. The dormant

sieve tubes deposit heavy masses of callose on the sieve plates, but these are removed during reactivation in the spring. The reactivated sieve tubes assume the same characteristics as the recently differentiated elements of the new season; that is, they show no nuclei, but have cytoplasm, slime, sieve-tube plastids and prominent connecting strands enclosed in relatively thin callose cylinders. These characteristics are exhibited by the phloem throughout the period of active growth of the plant, first in the reactivated, then in the newly differentiated sieve tubes. The interpretation of the enucleate sieve-tube elements as functioning seems well justified on the basis of the behavior of grape phloem.

SLIME BODIES AND SLIME. The occurrence of rather dense colloidal structures, the "slime bodies", in the cytoplasm of young sieve elements, and their eventual dispersal into the slime of a maturing element has been previously noted in many dicotyledons (see 33). Recently many additional dicotyledonous species have been shown to have slime bodies (95). The relative persistence of these bodies in the sieve tubes of certain Leguminosae has also been confirmed (95). Not all dicotyledons have equally large amounts of slime. In many tree species the sieve-tube protoplasts are very thin (92). The monocotyledons, the gymnosperms and the still lower vascular plants, in which slime bodies have not been recorded, have particularly thin sap with only small amounts of slime in their sieve elements (1, 33).

The slime bodies and slime are usually interpreted as being proteinaceous in nature. Recently Rouschal (92) reported having confirmed that this material is protein. Salmon (95), however, asserts that slime and slime bodies also contain lipoids, and calls the bodies "lipido-proteinaceous corpuscules" and the slime "lipido-proteinaceous accumulations". There appears to be no reference other than that of Salmon, which associates lipoids with the sieve-element slime. Lipoidal material was reported in phloem by Maugini (79), but not specifically in sieve tubes. Schmidt (98) and Rouschal (92) found none or very little fatty material in differentiated sieve elements.

The slime is assumed to be in dispersed or suspended state in the vacuole, but if the sieve element is cut, the slime accumulates on one or both sieve plates and forms here the so-called "slime plug". Recently Salmon (95) expressed the antiquated view that slime is

naturally located on the sieve plate and she interpreted this accumulation as plasma membrane.[4] According to Abbe and Crafts (1), the slime is transitory in nature and soon disappears from the sieve elements. Studies on phloem, which functions for more than one season (such as *Vitis* phloem), clearly show that the slime is relatively persistent and occurs in the sieve tubes during the first and in the subsequent season or seasons of their function. This observation agrees with an old conclusion of Fischer (48) that the presence of slime and the ability to form slime plugs are associated with the functioning state of the sieve tubes, while the disappearance of this substance indicates approaching obliteration.

In a rather limited study of sieve-tube protoplasts based on fixed material, Pigneur (86) found that the slime bodies of *Cucurbita* do not disperse but fuse into one mass. Such fusion of slime in *Cucurbita*—sometimes before dispersal in the vacuole, sometimes simply as a result of coagulation (especially often in fixed material)—had been previously reported in the literature (see 33). The structures, which Pigneur (86) interprets as slime bodies in *Athurium* and pictures as coalescing into small masses and threads, are very small and of a more definite shape than slime bodies usually are.

In *Vitis vinifera* slime bodies have been noted not only in the sieve tubes but also in the companion cells (42, 44). They disperse in the companion-cell protoplasts at about the time when the sieve-tube slime bodies break down. In the companion cell the dispersed slime appears to remain in the cytoplasm. Although the occurrence of slime bodies in companion cells seems to be unusual, the relative density of the companion-cell protoplast is a commonly noted characteristic. This density is a feature that is acquired during differentiation of the companion cell. Possibly, even if slime bodies do not appear as discrete structures in the companion cells, the same kind of substance develops in them in a more or less dispersed state and imparts the dense appearance to the protoplasts of these cells.

The term "slime" as applied to the colloidal and apparently proteinaceous material of sieve elements has been criticized by Schmidt (98) and Rouschal (92) chiefly because the substance is

[4] See the review of Salmon's paper by K. Esau in Bot. Gaz. **109**: 361-362. 1948.

not a true slime. Since, however, the exact nature and function of this slime is not yet known, phloem investigators are not ready to agree upon a more appropriate and a better-sounding term. (See also 42.)

PLASTIDS AND STARCH. Sieve elements of many species of plants contain plastids, the sieve-cell or sieve-tube plastids, which elaborate a carbohydrate giving a red staining reaction with iodine (33). The carbohydrate is regarded as being related to starch and may be referred to as "sieve-cell" or "sieve-tube starch". The wide distribution of sieve-tube starch in angiosperms has recently been confirmed by Salmon (95).

Apparently starch staining red with iodine is not restricted to sieve elements. Küster (70, p. 380–381) mentions such starch in the endosperm of some Gramineae, in the seed of *Sinapis*, in the root cap of *Allium cepa* and in some other structures and plants. It is supposed to contain much dextrin and amylodextrin. The red algae also develop starch that usually becomes red or reddish violet when treated with iodine and is doubly refractive. According to Fritsch (51, p. 410–411), some evidence suggests that this carbohydrate is allied to but not identical with the starches of higher plants. Guilliermond (55, p. 205) states that the Floridean starch is not formed in plastids and is capable of emerging into the vacuole—a characteristic sometimes ascribed to the starch grains of sieve elements.

The opinions regarding the exact location of plastids and starch grains in the sieve element are tied up with the controversy about the nature of sieve-element cytoplasm. Commonly in sectioned material the starch grains may be seen in Brownian motion in the vacuoles of the sieve tubes. The interpretation of this phenomenon by an early authority on plastids is of interest. Arthur Meyer (80) suggested that when phloem sections were placed in water, the sieve-tube plastids often were destroyed and the starch grains appeared in the cell sap where they showed motion. One should, therefore, according to Meyer, study only those sieve tubes whose contents are not in motion. In such elements the plastids appear near the walls or are piled near the sieve plates.

Among subsequent workers, some explain the presence of starch in the vacuole as resulting from the denatured state of cytoplasm; the boundary between it and the vacuole is supposedly obliterated,

the plastids break down and release the starch grains into the vacuole (see 33).

Rouschal (92), however, using special methods that enabled him to prevent the usual displacement of sieve-tube contents in sectioned material (see part on relation between structure and function of sieve element), found that the starch grains occurred within the parietal cytoplasm of mature sieve tubes, although very close to the periphery of the vacuole. By inducing a flow through the sieve tubes (adding glycerine on one side of the section), he easily dislodged the starch grains and observed their emergence into the vacuoles and accumulation at the sieve plates.

Sometimes starch is not characteristically present in the plastids. Thus in sugar-beet the carbohydrate was noted only after much material had been surveyed (34). Ordinarily the sieve-tube plastids of sugar-beet stain like cytoplasmic structures (33). The nature of the plastid-like granules in the sieve elements of monocotyledons and ferns is still uncertain (33, 95). Perhaps they are related to the elaioplasts described in some monocotyledons (45).

EXTRUDED NUCLEOLI. The sieve-tube inclusions mentioned under "unnamed inclusions" on p. 386 of the former review on phloem (33) have now been recognized as extruded nucleoli. The structures were first identified as such by Engard (31) in *Rubus;* however, he interpreted the free nucleoli as slime bodies. Esau (42) has shown that the extruded nucleoli are distinct from the slime bodies and that both kinds of structure occur in the same elements. The extrusion of nucleoli occurs during disintegration of the nuclei, and, while the rest of the nucleus disappears, the nucleoli remain in the sieve-tube elements as long as the latter exist as intact cells. The present writer (42) studied extrusion of nucleoli in *Rubus, Eucalyptus* and *Gossypium.* The globoidal inclusions observed by Crafts (20, 22) in *Casuarina, Melicytus, Populus* and *Tilia,* along with those in *Eucalyptus* and *Gossypium* are undoubtedly extruded nucleoli. These structures are readily identifiable in a photomicrograph of *Tilia* phloem given by Huber (62, p. 203, fig. 24) and in the illustrations of sieve-tube inclusions from *Althaea officinalis, Urtica dioica* and *Castanea vulgaris* in Salmon's (95) paper. The latter author did not determine the origin of the bodies and regarded them as slime bodies. Among the older writers, Lecomte (71) evidently saw extruded nucleoli

in *Tilia* and *Rubus* but he called them "albuminous globules". Apparently Fischer (48) too referred to extrusion of nucleoli when he said that in *Urtica* the nucleus seemed to dissolve incompletely, leaving as remnant a small disc-shaped structure.

The extruded nucleoli develop a peculiar external sculpture as soon as they leave the nucleus. They form protrusions of various degrees of fineness. In *Rubus*, for example, the protrusions are coarse and short, in *Eucalyptus* quite long and extremely fine (42).

The significance of the extrusion of nucleoli and of their retention after disintegration of the rest of the nucleus in the sieve tubes of some plants is not understood. The list of plants in which this phenomenon was noted thus far suggests that it occurs in widely separated groups of dicotyledons.

Older reports in the literature on the extrusion of nucleolar material into the cytoplasm concerned only dividing nuclei (73; also literature in 42). Recently, however, this phenomenon was described by Milanez (81) as occurring in the laticiferous tubes of *Hevea* during the disintegration of nuclei. As in the sieve tubes, the nucleolar material in the latex ducts is extruded in the form of one to several globules, successively or simultaneously.

STRUCTURE OF THE SIEVE ELEMENT IN RELATION TO ITS FUNCTION

THE SIEVE ELEMENT AS THE MAIN CONDUCTING STRUCTURE IN THE PHLOEM. Although many researches were concerned with the determination of the channels of migration of solutes and good evidence was assembled that the organic solutes move largely in the phloem, the first direct indication of this movement in the sieve elements was obtained only in 1930 by Schumacher (see 78.) By ingeneous operational procedures, this worker (102) was able to study separately the role of ground parenchyma, xylem and phloem in the removal of nitrogen from darkened leaves of *Pelargonium zonale*. His experiments showed that this movement occurs almost entirely through the phloem. In another experiment, eosin introduced into leaves was found to cause a callousing of sieve plates and an eventual collapse of sieve tubes and companion cells, without visibly injuring the phloem parenchyma. By treating with eosin *Pelargonium* leaves which were connected only by a

phloem bridge to the stem, Schumacher (102) succeeded in interrupting the removal of nitrogenous and other substances from the leaves. It seemed that the injury to the sieve tubes by eosin was responsible for the cessation of movement through the phloem. In his later experiment dealing with the movement of fluorescein in the phloem, Schumacher (103, 104) could observe microscopically that the dye was present in the sieve tubes and companion cells for long distances from the place of introduction of it into the plant.

IS THE SIEVE-ELEMENT PROTOPLAST DENATURED? Long before Schumacher carried out his investigations on the role of sieve tubes in translocation, the sieve element was generally considered to be the main conducting structure in the phloem. As was detailed in the previous review on phloem (33), some of the proponents of the mass-flow concept of translocation made determined efforts to correlate the structure and function of the sieve element, and their main conclusion was that the protoplast of this element was in a more or less passive state, particularly as expressed in its loss of the property of semipermeability. These efforts were continued during the last decade.

The investigators who were opposed to the concept of pressure flow in the phloem also renewed their observations on sieve elements in order to prove their idea that the protoplast of a functioning sieve element is active. This double attack upon the problem has brought to light new information on the cytophysiology of the sieve element.

The most consistent defense of the idea of permeability of the sieve-element cytoplasm came from Crafts. The previously reviewed microscopic studies of the phloem by this investigator (see 33) led to a formulation of the following concept (22). In the early ontogenetic stages the sieve element is a normal cell in its physiological responses. During maturation, however, the nucleus disintegrates and disappears; cytoplasmic streaming gradually ceases; the parietal cytoplasm loses its clear inner-phase boundary, and the vacuole its ability to accumulate vital stains; and the protoplast ceases to respond with plasmolysis to treatment with hypertonic solutions. Thus it appears that the cell becomes readily permeable to assimilates in solutions, permitting a free flow of sap through its lumen. In a much later paper Crafts (26) offers a

hypothesis on the submicroscopic change in the structure of cytoplasm to explain its permeability in the sieve element. He assumes a straightening of polypeptide chains during the process of denaturing, a loosening of bonds, and a loss of lipoidal substances responsible for semipermeable properties. There is supposed to be also a loss of polar groups and with it of the original staining properties. The lost substances are replaced by water, mostly in free state. Crafts concludes that such cytoplasm would offer little resistance to the flow of solution.

The morphological appearance of this cytoplasm is frequently considered by Crafts. In an early work the sieve-tube cytoplasm of potato is described as poorly delimited from the vacuole and appearing simply as a region of greater density or viscosity than the vacuole (see 33.) In the pine, too, the permeable sieve-cell cytoplasm is found to be very transparent and inconspicuous, though at the same time it is referred to as being tough and fibroid (1). In some other plants such cytoplasm is characterized as ductile, elastic, fibroid, tough and stringy (20, 21, 22, 26). It is found lacking in affinity for plasma stains. According to a personal communication from Dr. A. S. Crafts, the reference to the cytoplasm as being heavily stainable, in his paper on the survey of sieve elements in different groups of plants, 21, page 175, is erroneous. The statement should be "less heavily staining".

The significance of these variations in morphology—variations between a cytoplasm, which is only somewhat more dense than the vacuole, and the tough and fibroid structure—is not obvious from Crafts writings, and it is difficult to picture an elastic, tough and stringy cytoplasm as being poorly delimited from the vacuole.

Huber and Rouschal (65) made somewhat similar permeability and vital-stain-accumulation studies as Crafts and tended to agree with him on the interpretation of the nature of sieve-element cytoplasm. The concept of permeable conducting elements seemed to offer the best explanation of the mechanics of mass flow in the phloem. Münch (85), too, found this concept most useful, and in his last paper dealing with translocation emphasized that mass flow was determined primarily by two conditions: pressure differences and penetrability of the main conduits in the phloem.

As was brought out in the previous review (33), the results of Huber and Rouschal's (65) permeability studies were not entirely

unequivocal. These workers observed plasmolysis of mature sieve tubes in *Cucurbita* and had difficulty in obtaining uninjured preparations of *Robinia*, that is, preparations in which the sieve-tube contents were not displaced before the plasmolytic agent was applied.

The criticism has been raised that Huber and Rouschal misinterpreted the developmental state of *Cucurbita* sieve tubes, since their illustration of a plasmolysed mature sieve tube showed "an element with a relatively thin uncalloused sieve plate" (22). In reality the plate in the photograph in question is no thinner than is usually found in mature *Cucurbita* sieve tubes (see, for example, Crafts, 21, figs. 2 and 4).

The idea of permeability of sieve elements was soon challenged by Schumacher (105). He tested such elements in 27 different species in many families for their reactions to glucose and sucrose solutions, and reported that all could be plasmolysed at least once, and many could be deplasmolysed one or more times. To be sure that he was dealing with mature cells, Schumacher used, in some plants, elements that were previously found able to conduct fluorescein or elements in fully developed leaves with most of the phloem in differentiated state.

Schumacher (105) stressed the sensitivity of sieve elements to sectioning and cautioned about the exercise of extreme care in the manipulation of material in the study of plasmolysis. The latter usually begins in the median part of the sieve element and may quickly cause a contraction of the cytoplasm into a thin thread. If such a state is reached, deplasmolysis is not readily attained.

The possibility of disruptive action of sectioning upon the sieve-element protoplasts has been suggested in the literature before Schumacher. Crafts (20) replied that phloem cells other than the mature sieve elements were not injured by cutting and therefore the latter could be expected to be no more sensitive. It is well known, however, that the contents of mature sieve elements are readily displaced by cutting, whereas the other kinds of phloem cells are not so affected. The displacement certainly indicates a high sensitivity of mature sieve elements to mechanical manipulations, and Crafts (23) at least agrees that "cutting of sections for microscopic study destroys any conceivable mechanism for rapid phloem transport".

Although Huber and Rouschal (65) originally accepted Crafts' evidence on the permeability of the sieve-element cytoplasm, they were very much concerned about the displacement of contents of these elements in *Robinia* and suggested that the older sieve tubes of this plant might be so penetrable longitudinally ("wegsam") that they cannot be seen in uninjured state in sectioned material. The authors were certain that such sieve tubes were not functionless because phloem exudate could be obtained from them.

Similarly to Schumacher, Curtis and Asai (27) reported that when precautions were "taken to eliminate the disruption resulting from cutting the tissues before making the tests", the semipermeability of sieve-tube cytoplasm could be demonstrated. In the abstract where this report was made, the technical details of the experiment were not described, but according to a personal letter from Dr. O. F. Curtis to the writer the "precautions taken" were as follows: before the tissue was sectioned, its turgor was reduced by causing a severe wilting or by placing the stems, whose epidermis was scraped off, into strong sugar solutions. When such material was sectioned, the sieve-tube protoplasts appeared to have escaped disruption which commonly occurs when turgid phloem is cut. In another method the intact stems were placed into strong sugar solutions, usually about one-molal or stronger, and then plunged into boiling water. Controls were treated with boiling water only. Strong plasmolysis of sieve tubes was observed in the material pretreated with the sugar solution and none in the other.

Curtis and Asai (27) also contended that if the sieve tubes were permeable, their contents, because of high osmotic concentration, would plasmolyse the adjacent perenchyma cells. In support of this contention they stated that they had been able to plasmolyse phloem-parenchyma protoplasts in *Fraxinus* and *Cucurbita* by means of the respective phloem exudates from these two plants. Incidentally plasmolysis of mesophyll cells with phloem exudate taken from the same plants as the mesophyll was observed by Roeckl (91). It is problematical, however, whether this evidence of plasmolysis in tissue severed from the plant can be used to predict the possible situation in an intact plant. As is well known, the effects of cells upon each other are not determined solely by osmotic relationships. Huber (64), for example, assumes that the

effect of the osmotic concentration in the sieve elements is more than offset by the turgor pressure in them.

The reference to the absence of cytoplasmic streaming did not remain uncontested either. In a short paper, giving no cytological details, Small (108) reported having seen streaming in *Cucurbita* sieve tubes (interpreted as mature) in a thin strip of tissue connecting two parts of a stem of an intact plant growing in a pot. The strip was exposed for microscopic studies by cutting away the associated tissue. To reduce the operative shock, exceedingly sharp scalpels were used.

In contrast, Rouschal (92), who performed very intensive studies on sieve-element protoplasts, considered the loss of streaming a concomitant of other changes in the maturing cell.

Though occurrence of streaming, if present, would indicate that the sieve-element cytoplasm is rather normal, streaming as such is generally regarded as inadequate to account for the rapid transport observed in the phloem. Even some of the prominent advocates of a diffusional movement in the phloem hold this view (78, 103).

In view of the reports of Schumacher (105) and Curtis and Asai (27), the matter of permeability of sieve-element cytoplasm was obviously in need of further investigation. This task was undertaken by Rouschal in 1941 (92; see also reviews of this work in 63, 64).

This investigator considered first of all the question of sensitivity of sieve elements to sectioning by following the effect of this manipulation upon the phloem in different developmental stages. The familiar displacement of contents of sieve elements began to appear in the sieve tubes of *Robinia* before breakdown of the nucleus, but after the cytoplasm changed its appearance from coarsely granular to very thin and filmy and the sieve-area pores became clearly evident. Peculiarly Rouschal uses the expression "when the sieve pores are broken through". The highly sensitive cytoplasm is characterized as being labile.

In his studies on plasmolysability of sieve elements, Rouschal used two gymnosperms, some dicotyledonous trees and *Cucurbita pepo*. Glycerine, grape sugar, $CaCl_2$, $AlCl_3$, KNO_3, and KCNS were used as plasmolytic agents. In all instances the sensitivity of the sieve elements to sectioning interfered with successful

demonstration of plasmolysis. Rouschal then devised a pretreatment, a "preplasmolysis" of phloem in intact state to reduce its turgor before sectioning. The dead bark was removed in a small area, but the functioning phloem was left protected by some living parenchyma cells. Then a paraffin cup containing a glycerine solution was fastened to the exposed area. The cup was cut out on the side turned toward the tree so that the glycerine came in contact with the living cells. In *Cucurbita* the glycerine was injected into the hollow pith area of stems and petioles. This pretreatment did not cause plasmolysis, but made the sieve elements less turgid, and as a result a much greater number of these elements remained intact and could be successfully plasmolysed. Similar results were obtained in the pine by a pretreatment consisting of a hardening of the phloem by $AlCl_3$ and $CaCl_2$ solutions used in place of glycerine. Author mentions also a successful deplasmolysis obtained in his studies.

In considering the details of the plasmolytic reaction of sieve elements, Rouschal stated that during plasmolysis the cytoplasm remained attached to the sieve areas. In other words, the sieve areas constituted the negative areas of plasmolysis.

Although Rouschal was able to induce plasmolysis in mature sieve elements, he continued to regard the latter as highly penetrable, at least in the sieve areas. To test this concept he pretreated with glycerine some phloem of *Aesculus,* prepared sections from it, then introduced some glycerine under the cover glass on one side of the section. Thus a one-sided suction was established and the sieve-tube contents exhibited a rapid longitudinal movement through the vacuoles without any evidence of separation of the cytoplasm from the lateral walls. The flowing sap dislodged the starch grains from their parietal position in the cytoplasm and carried them through the vacuole toward the sieve plate.

According to Rouschal, this experiment demonstrated for the first time, under the microscope, the occurrence of mass flow in living sieve tubes and furnished additional proof of a specific longitudinal penetrability of these elements. He felt justified in concluding that the cytoplasm on the sieve plates was more permeable—at least for water—than the lateral layers.

The glycerine treatment just described failed to cause a longitudinal flow if the sieve plates were plugged (presumably with the

proteinaceous material, or the slime; author does not go into the details of this supposed plugging). Rouschal suggests that such plugging is a prerequisite for a successful plasmolysis of sieve elements. If the sieve areas are not plugged, the flow of sap through these areas after sectioning causes the displacement of contents. In natural state, Rouschal contends, the mechanism of plugging may be a means of preventing a loss of materials from sieve elements opened accidentally. Münch's (84, p. 130) observations on the eventual restoration of turgor in phloem that had been incised for obtaining exudate, is supposed to agree with this contention.

Referring to the relative impermeability of the lateral cytoplasm, Rouschal (92) recalled that Münch assumed the existence of such impermeability because he thought the sieve elements occurred next to intercellular spaces. The occurrence of intercellular spaces in the phloem has been reported in the literature, but the phloem has also been described as a compact tissue resembling collenchyma (33). Recently Martens and Pigneur (76) considered this point in some detail by examining phloem of 25 species of dicotyledons and gymnosperms. They used fresh free-hand sections treated with Eau-de-Javelle. Eleven species contained intercellular spaces in the phloem sufficiently close to the cambium that they could have been assumed to be in the functioning part of the tissue; the other 14 did not. Some intercellular spaces occurred next to sieve elements.

Rouschal (92) reinvestigated the reaction of the phloem to neutral-red treatment. He stained the tissue in the tree and in severed sections. In both conditions differentiated sieve elements did not accumulate neutral red, and this property appeared even before the cells were fully mature. The same sieve elements which failed to accumulate the dye could be plasmolysed. Using fluorescence microscopy, Rouschal checked the possibility that the sieve elements, because of their alkaline sap, might accumulate the base of the dye rather than the dye itself. No such base accumulation was detected in mature sieve elements. The young elements and the cambium contained both the dye and the base of the dye.

Rouschal assumed that the failure of mature sieve elements to accumulate neutral red resulted from a combination of alkaline

state and scarcity of fatty substances and tannins. His own tests for lipoidal substances with OsO_4 gave a slight darkening of cytoplasm and no color reaction in the vacuole. Preliminary tests with rhodamin B also gave negative results regarding presence of lipoids. Among the preceding workers, Schmidt (98), too, found no accumulation of fatty materials in the sieve tubes. As mentioned earlier, Salmon (95) claimed to have found a progressive increase of lipoids in the slime of differentiating sieve tubes.

That tannins play a role in the accumulation of vital dyes in certain type of vacuole is well known (130). Lipoids, on the other hand, are usually associated with the cytoplasm rather than the vacuole. However, Bailey and Zirkle (6, 130) think that fatty substances may well exist in the vacuome, and Scarth (96) has shown that in certain vacuoles the colloidal contents act as partially hydrated lipoids. Regarding the effect of pH, Zirkle (130, p. 9) states that neutral red "does not collect in vacuoles more basic than pH_6".

Although the behavior of the fatty materials in the differentiating sieve-element protoplast needs further study, observations made thus far indicate, according to Rouschal, that during maturation, fatty acids and neutral lipoids diminish in amount and the protoplast and cell sap become more and more hydrophilous. The alkalinity of the sap may also favor hydration, especially since K alkalies prevail. Rouschal finally concludes that the hydration of cytoplasm is responsible for its labile state, its low viscosity and highly fluid condition, and its appearance as though it were optically empty when examined with surface illumination. Huber and Rouschal (65) and later Rouschal (92) attempted to study sieve elements in their natural position in a plant by fastening a dark field microscope to a tree. The contents of parenchyma cells were discernible, but the sieve elements appeared optically empty.

Crafts' (26) idea of a viscous, tough, fibrous condition of the sieve-element cytoplasm obviously conflicts with Rouschal's (92) picture of a highly fluid fine ("zart") cytoplasm, thin as breath ("hauchdünn"); but the thinking of the two investigators converges on the concept of a highly hydrated state of this cytoplasm.

According to Rouschal (92), one of the most important unexplained matters regarding the cytophysiologic characteristics of the sieve element is that of the relation between the vacuole and

cytoplasm; in other words, the matter pertaining to the nature of the tonoplast. He was unable to detect a tonoplast in any experiments. In connection with this problem, the cause of the high permeability of the cytoplasm at the sieve areas also cannot be fully explained at present. Moreover, this permeability has been experimentally shown to exist for water and fluorescein alone, whereas passage of sugar and protein precursors can be only assumed from the physiologic evidence of movement of materials through the phloem.

In contrast to Rouschal, a student of Schumacher, A. Schumacher (101) reported having found evidence of the existence of a tonoplast. Similarly to Schmidt (98), she described cytoplasmic strands crossing the vacuoles. However, author found these structures in relatively few sieve tubes and did not mention the stage of development of these elements.

While the plasmolytic studies of W. Schumacher and Rouschal contradict the idea of passivity of the sieve-element protoplast, the investigations of Roeckl (91), a student of Huber, supply new evidence that the movement from the mesophyll toward the phloem does not follow a gradient from a relatively high to a relatively low pressure. In a detailed study of the osmotic relations in the mesophyll and phloem, Roeckl found a gradually but noticeably increasing osmotic pressure from the palisade parenchyma, through the collecting cells (50, p. 126) of the spongy parenchyma and the border parenchyma of the bundles, toward the phloem. Thus the movement from the place of elaboration of carbohydrates to the sieve elements seems to occur against the concentration gradient.

THE SHAPE OF SIEVE ELEMENTS, AND ITS RELATION TO FUNCTION. In Crafts's (22) opinion the shape of the sieve elements and the structure of the sieve plate are of little consequence with regard to translocation; these elements are assumed to have cytoplasm as permeable as the walls, permitting therefore ready passage of inorganic nutrients and organic assimilates, regardless of the presence of sieve plates. Recently he (26) developed this concept further by suggesting that, like the cytoplasm, the sieve-element walls too may be highly hydrated and permeable, and therefore specialized for conduction.

The German phloem investigators did not adopt Crafts' view on the unimportance of sieve plate in translocation and continued to

search for the significance of size and distribution of the sieve areas in the sieve elements, of the pores in the sieve areas, and of the variations in these characteristics. Huber (62) was concerned about the observed trend in the evolution of the sieve elements from long-spindle-shaped cells to short elements with more or less transverse end walls; in other words, a trend toward an increase in the number of sieve plates to a unit of length of the phloem strand. He concluded, however, that no actual increase in resistance to flow resulted from this evolutionary sequence because of the concomitant widening of the elements and particularly because of a change from many small to few large pores in the sieve plates. This trend, according to Huber, answers the demands of the law of Poiseuille for mass movement. Münch (85), concurring with Huber, made detailed calculations of possible rates of movement, considering the width of the sieve elements, the number, diameter and length (corresponding to thickness of sieve-area wall) of pores, and concluded that in the angiosperms and gymnosperms the area covered by the pores is approximately as large as the transection of the sieve element.

In contrast, Schumacher (101) found in *Bryonia dioica* that the sieve-plate pores, including the callus cylinders, occupied only 46 to 68 per cent of the sieve-plate area. If measured within the callus cylinders, the pore area is reduced to from four to six per cent of the sieve-plate area. The last values closely approach those previously obtained by Crafts (19) for potato sieve tubes; in these the strands were reported to occupy 2.3 per cent of the sieve-plate area. Schumacher (101) emphasized that while the sieve-tube lumen was reduced within the pores, the internal surface, that is, surface covered with cytoplasm, was increased two to four times.

Cheadle and Whitford (15) suggested that the orientation of the sieve plates has some bearing on the efficiency of sieve tubes in conduction. Since they found sieve-tube elements with transverse end walls and simple sieve plates in leaves, in annual and storage organs, and in plant groups which seem to have highly specialized vascular elements in general, they advanced the notion that such sieve-tube elements are highly specialized with regard to food conduction.

The proper conclusion regarding the role of the shape of the

sieve element in the performance of its function will not be drawn, of course, until this function is properly understood.

THE NATURE OF CONNECTING STRANDS. The question whether the connecting strands in the sieve areas are purely cytoplasmic or whether the vacuolar contents are also connected through the pores has played a prominent part in the speculations about the function of the sieve-element. To interpret the connecting strands as cytoplasmic and to refer to them as "plasmodesmata" has become rather common in modern phloem literature (22, 33, 66, 78, 92). In contrast, some of the old workers assumed continuity of vacuolar contents through the pores in uninjured sieve elements.

According to the concept of Crafts (22, 26), the absence of vacuolar connections through the pores in the sieve areas would not prevent free flow across the plate because the cytoplasm and the wall component of the sieve area are both highly permeable.

Without referring to Crafts, Rouschal (92) expressed a somewhat similar idea when he stated that the submicroscopic pores of the cell walls would suffice for movement of water and sugar across the sieve areas, especially in view of the evidence of high cytoplasmic penetrability in these areas. Nevertheless, he also speculated on the possible structure of the connecting strands that may make them permeable: perhaps these strands were composed not of semi-permeable membrane alone but of inner cytoplasm delimited by a membrane along the pore walls. Thus at least one semi-permeable barrier would be non-existent. Absence of a tonoplast would further increase permeability.

The sieve-element slime is commonly present in the sieve-plate pores in sectioned material. Such distribution of this matter has been interpreted as an artifact in most of the modern and some of the old literature (see 33). Recently, however, Schneider (100) thought he saw evidence of normal continuity of slime between elements. In *Vitis* used by the present writer (44) occasional dormant sieve tubes had dense masses of slime stretched through the whole length of the elements and connected by single thick strands through the sieve plates. The latter were covered with thick dormancy callus at this time, except where the strands occurred. These views did not suggest a response "to intense and sudden steepening of the pressure gradient by cutting" (21), since the sieve tubes were in dormant state and the slime did not occur

as "slime plugs" on the sieve plates. Possible normal association of the slime with the sieve plate perforations in *Vitis* is also indicated by the reappearance of slime strands in the callus during reactivation of the sieve tubes. These strands become evident before the dormancy callus is removed, and at first they penetrate the callus mass only part way (44, plate 20, *A*), sometimes from both sides at the same time.

Another significant observation is that the characteristic chromaticity of the connecting strands in the differentiating sieve elements and the firm attachment of the protoplast to the sieve plate become evident approximately at the time when the nucleus and slime bodies disintegrate (32, 44). Moreover, only the connecting strands show the increased chromaticity, whereas the cytoplasm along the lateral walls remains lightly stained. If the dense staining of the connecting strands occurs because the cytoplasm composing them shows affinity for dyes (26), then one should assume that this cytoplasm differs from that in the parietal layers which lose their chromaticity during maturation (26). An alternative possibility would be that the slime is in some way associated with the cytoplasm of the connecting strands and makes them chromatic.

Occasionally the literature reports that the connecting strands in the sieve areas are not continuous. Mangenot (75), for example, considered both the pit connections in red algae and the sieve-plate connections in dicotyledons as discontinuous structures. According to many workers (see 51, p. 447), the pits in the Florideae have pit-closing membranes with fine plasmodesmata connecting the masses of cytoplasm that fill the pit cavities. Mangenot calls these masses "plasmodesmata", denies the presence of pit membranes and suggests that the "plasmodesmata" are individually invested in their own plasma membranes. From a brief study of sieve tubes of some angiosperms he drew a similar conclusion about the connecting strands in the sieve plates; in some plants he saw a light line in the median part of each connecting strand and interpreted this line as a discontinuity. Salmon (95) followed Mangenot in describing the connecting strands in the sieve plates of angiosperms as being double, though she too found the "light line" dividing the strands in halves an inconsistent characteristic.

It is of interest to recall that the earliest workers on phloem macerated this tissue and pictured very much extended but uninterrupted connecting strands of sieve plates in which only the intercellular substance or all wall substances were removed (57, 59, 125; see also 33, fig. 3).

SIZE OF THE SIEVE-TUBE SYSTEM AS A WHOLE. A unique attempt to relate the dimensions of the entire sieve-tube system of a plant to the activity of this system, as expressed in the conduction of fluorescein, was made by A. Schumacher (101), a student of W. Schumacher. The number of sieve tubes, their transsectional areas and the length of their elements were determined at different levels of several herbaceous and woody plants. The values for the transsectional area and length of elements served to calculate the volume and the internal surface (surface of the lateral walls and of the two sieve plates) of the sieve elements.

One of the staminate plants of *Bryonia dioica* which was studied in particular detail gave the following values. The main axis of the plant was 7.4 m. long and bore 73 leaves, 73 tendrils, 28 inflorescences and five lateral branches. The latter taken together were 13.8 m. long and bore 140 leaves, 140 tendrils and 44 inflorescences. The counts and measurements were made a few cm. apart in all organs of the plant including the roots. The calculated totals indicated the presence of approximately 80 million sieve-tube elements in the entire plant. These had an internal surface of one sq. m. and a total volume of only four cubic cm.

In the main axis 300 to 400 sieve tubes were found in one transsection. In one centimeter of stem these sieve tubees occupied a volume of two to three cubic millimeters and had an internal surface of 300 to 400 square millimeters. This surface exceeded the outer stem surface three to four times.

In the longitudinal course through the main stem and the tap root, including the enlarged part of the latter, the volume and the internal surface of the sieve tubes decreased toward the apices. The number of the sieve tubes diminished only slightly in the stem, very strongly in the root. In the lateral organs the conducting elements were of smaller dimensions than those in the main axis and were reduced in volume and internal surface toward the apices.

The volume of the sieve tubes in the main axis was about equal

to that of the entire lateral system, but the latter had a three times larger internal surface in all its sieve tubes. Thus the downwardly moving materials would encounter no reduction in relative volume, but a decrease of internal surface in the part of the conducting system where the lateral branches join the main stem.

Author also studied the movement of fluorescein in various parts of *Bryonia dioica* plants, related this movement to the size relationships in the sieve-tube system and suggested that the cytoplasm proper may play an important role in the transport of assimilates.

CONCLUSIONS. The data reviewed show that the opinions regarding the characteristics of the protoplast of a sieve element continue to be divided. Most evidence suggests that the mature functioning sieve element has no nucleus; that its vacuole is not clearly defined; that it is very sensitive to mechanical manipulations and responds to these with a marked displacement of its contents; that when special precautions are taken to preserve the protoplast in its natural state, it can be plasmolysed and even deplasmolysed, but cannot be made to accumulate vital stains; and that there is at least a cytoplasmic continuity from element to element.

Although it is commonly accepted that materials move rapidly through the sieve elements, the views of the proponents of the mass flow and of those of a diffusional movement are not reconciled about the particular characteristic which determines the rapid movement. There is experimental evidence, however, that materials pass readily across the sieve areas.

PHLOEM DEVELOPMENT

PRIMARY PHLOEM. The basic features of the development of primary phloem and the concepts of protophloem and metaphloem have been discussed in detail in two reviews by the writer (33, 38). Since then several new articles dealt with vascular initiation and have furnished data which are in general agreement with the conclusions drawn previously.

Firstly, in a growing shoot or root the initial sieve elements mature closer to the apices than the initial tracheary elements; in other words, within the procambium the first sieve elements appear earlier than the first tracheary elements at a given level of

stem or root. Such timing in vascular differentiation has been recorded in the shoots of gymnosperms (24, 25, 56, 110, 111), dicotyledons (31, 35, 41, 44, 82, 89, 100) and monocotyledons (40, 106), and in the roots of various plants (39, 126). Not all the references just cited give an accurate description of the first sieve elements. Usually, however, the latter can be identified as such in the accompanying illustrations by the similarity in position and appearance with elements that have been definitely recognized as sieve elements by some other writers. Papers presenting contrasting views, that xylem elements differentiate before (10) or simultaneously with (17) the first phloem elements, give no satisfactory evidence that the initial sieve elements were actually seen by the authors.

Secondly, in gymnosperms and dicotyledons the first sieve elements show a usually continuous acropetal differentiation within the shoot axis and from the axis into the leaves (24, 25, 31, 36, 41, 56, 82, 89, 110, 111)[5]. In their acropetal differentiation the sieve tubes may show discontinuous maturation. Thus in both flax and sunflower studied by the present writer (36, 41) some leaf traces showed series of immature sieve-tube elements interpolated between series of mature ones.

The sequence of protophloem, metaphloem and secondary-phloem development was investigated in detail by Schneider (100) in the peach and by Esau (44) in the grapevine. In both plants fibers differentiate in the protophloem after the sieve tubes are obliterated. The metaphloem has no fibers. This pattern of differentiation is in keeping with that established for many other dicotyledonous plants (33). Schneider (100) points out that in the leaf blades and petioles of peach the protophloem cells other than the sieve-tube elements elongate much but do not complete their development into fibers; they remain without secondary walls. This difference in the characteristic of the old protophloem in leaves and stems is common in dicotyledons and is well illustrated by *Nicotiana* (32), *Cannabis* and *Corchorus* (69).

Schneider (100) has found, in the peach, a lag between the

[5] According to recent studies (64*a*), the protophloem and metaphloem in the internodes of *Equisetum* differentiate basipetally. This course of differentiation appears to be related to the protracted intercalary growth at the base of the internodes. It would be of interest to determine the course of phloem differentiation in monocotyledons having a similarly prolonged intercalary growth of internodes as *Equisetum*.

initiation of the last metaphloem cells and the start of production of secondary phloem. Moreover, the last cells initiated on the phloem side by the procambium matured as large parenchyma cells, and thus the metaphloem became sharply delimited from the secondary, at least in the internodes. Whether the two kinds of tissue are interconnected in the nodes has not been investigated.

SECONDARY PHLOEM. The seasonal development of the secondary phloem has received some attention in the new literature. The research previously reviewed by the writer (33, pp. 419–421) and certain other references (67, 87, 100) suggest that in most angiosperms the secondary phloem functions only one season, but some cambial derivatives on the phloem side pass the winter in undifferentiated state and complete their maturation in the spring before the cambium resumes its activity. Huber (62) reexamined the seasonal changes in several dicotyledonous and gymnospermous trees. By using mainly transverse sections from material preserved in alcohol, he determined how much of the phloem contained collapsed sieve elements at different times of the year. Callus development and changes in contents of the cells were not followed in detail. According to Huber (62), in the dicotyledons either all sieve tubes are collapsed before the cambium is reactivated or a few of the last-formed narrow sieve tubes are still open. This observation agrees with that of Gill (53) who also found, in *Fraxinus excelsior* and *Quercus robur,* some narrow-celled autumn phloem which was not crushed until the second season of its existence.

In certain Abietineae Huber (62) observed that a considerable part of a season's growth remained intact through the winter and did not collapse until late in the second season. Thus in a given growth season the active phloem band was eventually made up of two parts formed during two successive seasons. In *Picea excelsa* the latest row of cells of a given season collapsed in the spring and could be used as a marker between the two different parts.

Apparently the sequence in the seasonal development of the Abietineae phloem, reported by Huber (62), is not generally known. Raatz (88), however, seems to have referred to the same phenomenon in 1892 when he mentioned the persistence of sieve cells in *Picea excelsa* and the collapse of the latest row in a given season's increment before the beginning of new growth. Brown's

(13) description of phloem development in *Pinus strobus* implies that part of a season's growth does not collapse in the fall and survives through the winter. He calls this tissue "transitional cells". According to Abbe and Crafts (1), in *Pinus strobus* some sieve elements remain immature during the winter and then complete their development in the spring.

As a side issue of his studies on the plasmolysability of sieve elements, Rouschal (92) noticed that in trees this property changed strikingly during the course of one summer. Plasmolysis was easy to demonstrate till the end of July. After this time the protoplasts became very sensitive to sectioning. This change occurred in the phloem that was formed during the season when the tests were made and, in *Pinus*, also in those elements that were carried over in a non-collapsed state from the season before. The increase in sensitivity of the sieve-element protoplasts appeared to coincide with the beginning of the state when exudate could be obtained from the phloem. Huber (64) finds no explanation for this late start of exudation in trees, but sees in it an indication of a lack of exact parallelism between movement of assimilates and occurrence of exudation.

According to the literature just reviewed, the secondary sieve tubes of dicotyledons are commonly short lived and become functionless during the same season when they are initiated in the cambium. Because of the relative longevity of their sieve elements, *Tilia* and *Vitis* are the recognized exceptions among the dicotyledons (33, 62). In *Tilia* the sieve tubes are reported as remaining active for several years without development of callus during the winter. *Vitis* sieve tubes, on the contrary, deposit large masses of transitory (or dormancy) callus as the plant becomes dormant and remove this callus again the following spring (44, 125). In other words, *Vitis* phloem shows an alternation of dormancy and reactivation, and these phenomena may occur more than once in the same sieve tubes (44). Usually, however, the sieve tubes of *Vitis* cease to function during the second summer after they are formed, and the inactive phloem is cut off by cork. Definitive callus may or may not develop before the elements cease to function.

Apparently, besides *Vitis*, only *Tecoma* and certain monocotyledons have been observed forming transitional callus during the winter dormancy (see literature in 33, 44.) Although

Bliesenick (9) spoke of resumption of activity in the spring by the old sieve elements, as though it were a common behavior in many plants, he failed to distinguish between transitory and definitive callus—at least, he did not mention the latter in describing phloem obliteration. His reports on reactivation require, therefore, a reexamination.

FUNCTIONLESS PHLOEM. The terms "nonfunctioning" or "functionless phloem" are commonly used to designate a tissue that ceases to be concerned with the primary function of the phloem, viz., conduction of organic solutes (33, 44). The sieve elements and companion cells (or their analogues) are dead and more or less collapsed in such phloem, but the other parenchymatous elements or other types of living cells (e.g., septate fibers, 44) continue to take part in the metabolism of the plant. This is evidenced by starch storage in them. Thus the difference between functioning and nonfunctioning phloem is determined by the condition of the sieve elements and the cells specifically associated with them.

The characteristics of non-functioning phloem vary in different plants. The appearance of the primary phloem after it ceases to conduct has been considered in the previous review (33) and also in the parts dealing with phloem fibers and primary phloem in the present paper. Commonly the primary sieve elements (and companion cells, if present) are more or less crushed or entirely obliterated by pressure from the surrounding cells. Crushing of sieve elements occurs in the secondary phloem also. If the latter contains many fibers, the sieve elements may remain open, but devoid of their original contents (e.g., 44, 52, 100).

Vitis appears to be the only plant recorded in the literature as having tyloses in old sieve tubes (44, and the literature reviewed there.) These tyloses arise from phloem-parenchyma cells in the part of the functionless phloem that fails to be cut off by the cork cambium. They store starch and sometimes develop thick walls.

Commonly definitive-callus formation accompanies the loss of function by the sieve elements, whether this loss occurs normally or under the influence of diseases or other injurious agents (43, 102). If the functionless phloem is not quickly sloughed off, the definitive callus may be again removed. How this removal occurs in the presence of a disorganized protoplast is not clear.

The death of companion cells in angiosperms and of albuminous

cells in gymnosperms has been emphasized in the previous review (33).

In contrast to all other reports on inactive sieve elements, Shimakura (107) contended that in the rhytidome of conifers the sieve cells, as well as the phloem parenchyma, underwent expansion. Normal sieve cells were neither pictured nor described by this writer, and the identity of these cells in his illustrations of the rhytidome is very uncertain. The expansion of phloem-parenchyma cells in the non-functioning phloem is a familiar phenomenon. It appears to be the primary cause of crushing or obliteration of sieve elements (33). The latter, however, as enucleate cells are not known to be capable of further growth after the loss of nucleus.

PHLOEM DEVELOPMENT IN RELATION TO FLOWERING. Wilton, Struckmeyer and Roberts reported in a series of papers (112, 113, 128, 129) that the essential anatomic characteristic of the flowering stems of herbaceous plants is the slowing down or, if reproductiveness is strongly expressed, a complete cessation of cambial growth. As a result of this interruption of meristematic activity, xylem and phloem mature to the cambial initial zone. The phloem of reproductive axes shows fewer and smaller cells than those of the vegetative. In general this tissue appears in flowering axes quite mature and even senile because of the thick walls, the pronounced callousing of sieve plates and the marked crushing of sieve tubes (90, 113). The cessation of cambial activity and the concomitant phenomena spread downwards in flowering axes (128). A renewal of vegetative growth is accompanied by a resumption of cambial activity (113, 114, 129). The anatomic modification characteristic of flowering plants can be quickly induced by placing plants in environment favorable for flowering, and the changes occur before flower primordia become microscopically discernible (112).

By comparing the anatomy of leaves in topped and untopped tobacco plants, Avery (5) found that vegetative growth ceased soon after the seeds started to form. Topping stimulated cambial activity which, however, resulted in xylem production only. Phloem cells, on the other hand, developed in greater numbers in untopped plants forming seeds. Thus Avery's data regarding phloem differentiation in fruiting and nonfruiting plants seem to

differ somewhat from those of Wilton, Roberts and Struckmeyer (112, 113, 128, 129). Whether this difference is a result of the use of different kind of material in the two sets of studies (Avery using leaves, the others stems) is not obvious at present.

The data on phloem development in relation to flowering in woody species are incomplete. In the alternately bearing apple, the spurs that initiate flower primordia on a non-bearing tree ("off-year" spurs) show the flowering type of anatomic structure four to five weeks before the primordia are apparent (115). Although cambial activity ceases early in such spurs, Finch's (47) observations indicate that the initial radial growth proceeds in them so vigorously that they have in the end a much wider increment of xylem than spurs not forming flower primordia. Whether the phloem too is wider in the spurs that are preparing for fruit-bearing is not indicated. Even if this phloem were wider, it could become functionless at the end of the season. Then, presumably, cambial activity in the same spur would form new phloem at the beginning of the new season, the season when the flowers would expand. Apparently this particular matter has not been investigated in the apple. In an early paper Finch (46) reported that cambial activity in "one and two year old wood" of non-bearing trees started later but proceeded more rapidly than in similar "wood" of bearing trees. He did not specify, however, whether this "wood" was part of the fruiting spurs in the bearing trees.

Gill (54) found considerable differences in the relation between flowering and cambial activity in different amentiferous tree species. *Corylus avellana* and *Alnus glutinosa* have fully differentiated catkins at the beginning of the winter, and their expansion in the spring is associated with no renewal of cambial activity in the inflorescence axis. In contrast to these two species, *Populus serotina* and *Salix caprea* have, during the winter, rather undifferentiated catkins, and when the latter expand in the spring renewed xylem and phloem differentiation occurs in their axes; furthermore, some phloem (but no xylem) differentiates also throughout the twigs below the expanding catkins.

The physiologic implication of these various observations has not yet been properly interpreted. The discontinuance of cambial growth in flowering stems of herbaceous plants, as emphasized by

Wilton, Struckmeyer and Roberts, suggest that maturation of vascular tissues is a concomitant of the initiation of the reproductive state, whereas the vegetative condition is associated with continued formation of vascular elements. In the woody species, too, a cessation of cambial activity and of growth in length occurs in the preparation for flowering. But flower primordia are initiated in one season and fruits develop in the second. The behavior of the cambium of a fruit-bearing spur (the cambium which early ceased its activity during the previous season) and the condition of the phloem of such a spur is apparently not known.

PHLOEM FIBERS

PRIMARY-PHLOEM FIBERS. Considerable information has been gathered during the last ten years proving that the fibers occurring on the periphery of the vascular system in many dicotyledonous stems (the "pericyclic" fibers) are primary phloem fibers (see 37, 44, and the literature reviewed there.) In other words, these fibers arise from the same part of the procambium as the earliest sieve tubes, and the latter usually occur among the cells that subsequently mature into fibers. During elongation of the organ in which they differentiate, the first sieve tubes are more or less obliterated and the fibers mature by ceasing to elongate and by developing secondary walls. This sequence of development has been observed during the last few years in *Cannabis* and *Corchorus* (52, 68), *Linum* (37), *Prunus* (100), *Cryptostegia* (4) and *Vitis* (44). The phloic[6] origin of the peripheral fibers has been previously discussed by the present writer in relation to the question whether or not these fibers should be termed "pericyclic" (33, 37, 38, 44).

If the primary-phloem fibers are considered in the light of the concepts of "protophloem" and "metaphloem" (38), they appear to fit best into the category of "protophloem fibers" because they and the sieve tubes associated with them are initiated before the elongation of organs in which they occur. The subsequent phloem, the metaphloem, whose sieve tubes mature after the organs elongate and persist longer than the protophloem sieve tubes, is

[6] This term is used as proposed by Esau (44): "The word 'phloic' is adopted here as an adjective derived from the word 'phloem'. A precedent in the use of the adjectival form of 'phloem' occurs in the well known terms 'ectophloic' and 'amphiphloic' ".

usually free of fibers, especially if fibers occur in the protophloem (33).

The differentiation of most or of all cells that remain intact in the protophloem after obliteration of the sieve tubes raises a provocative question regarding the possible functional relation between the future fibers and the protophloem sieve tubes while the latter are still intact. These sieve tubes, especially the earliest among them, may be without companion cells (33). Students of phloem usually think of the function of sieve tubes as being at least partially controlled by the normal nucleate cells associated with them. Perhaps the future fibers, which appear to be the only nucleate cells in the protophloem of some plants, play a similar role in the function of this tissue as phloem parenchyma or even companion cells.

The cells acquiring secondary, often lignified walls in the old primary phloem sometimes do not develop into typical fibers; they remain relatively short and their ends do not become much pointed. It seems entirely proper to regard these cells as sclerified phloem parenchyma. Wilson (127) treated thus the lignified cells of the primary phloem of the many Compositae which he studied. Russow (94) considered that the thick-walled lignified cells in vascular bundles of some Compositae, Gramineae, Liliaceae and Aiismaceae are not "Bastzellen" but are derived from the "Weichbast"; that is, they are simply the modified parenchymatous elements of the phloem.

Whether there is any fundamental difference in the physiologic relation between the sieve tubes and young fibers on the one hand and between the sieve tubes and phloem parenchyma (which may or may not become sclerified) on the other, is a question that cannot be answered. At present one can only record the existence of variable development of the sclerenchyma during primary vascular differentiation. In some plants the strengthening cells are initiated as such very early and eventually develop the characteristics of typical phloem fibers (e.g., *Linum, Cannabis, Cryptostegia*); in others the supporting tissue differentiates "secondarily" from phloem parenchyma (e.g., certain Compositae); in still others sclerenchyma arises not in direct association with the vascular tissues but outside of them (e.g., *Cucurbita, Aristolochia, Tradescantia*).

SECONDARY-PHLOEM FIBERS. In the previous review on phloem (33) a positive statement appears on page 412 that "the ontogenetic relation between the fibers and the other members of the secondary phloem is clearly understood. When present, the fibers arise, together with the other elements of the longitudinal system, from fusiform initials of the cambium". Since these lines were written, a different, although not a new, aspect of fiber development in the secondary phloem has attracted reviewer's attention. In some species the secondary phloem shows no fully differentiated fibers while the sieve tubes are in functioning state. Only after the latter become senile, fibers mature. In the cherry (100) and guayule (3), for example, sclerification of the secondary fibers is delayed until the sieve tubes cease to function. In guayule it seems impossible to distinguish between the phloem-parenchyma cells and the "sclerenchyma initials, since most of these cells are pointed and eventually thicken and lignify" (3). Perhaps fibers, while not fully mature, sometimes replace phloem parenchyma in the secondary phloem as they appear to do in the primary.

Generally developmental relations suggest the following three categories of fibers in the secondary phloem: (*a*) fibers maturing at the same time as the sieve elements and appearing to be highly specialized as mechanical elements (e.g., *Tilia*); (*b*) fibers maturing at the same time as the sieve elements but retaining active protoplasts that are concerned at least with the carbohydrate metabolism (e.g., starch-storing septate fibers of *Vitis*); (*c*) fibers maturing after the sieve elements cease to function and sometimes resembling the phloem parenchyma cells in the functioning part of the phloem (e.g., cherry, guayule).

Thus the statement made ten years ago and cited in the beginning of this section of review must be revised as follows: "The ontogenetic relation between the fibers and the other members of the secondary phloem is not always clearly understood, since in some plants the fibers mature late and cannot be distinguished from phloem parenchyma in the functioning part of the phloem". The commonness of the loss of protoplasts by fibers (33, p. 413) may be questioned also in view of Kundu's (68, 69) report that even such typical phloem fibers as those of *Cannabis* and *Corchorus* remain alive throughout the life of the plant.

PRIMARY-PHLOEM FIBERS AND THE PERICYCLE. As was previously implied in this review, identification of primary-phloem fibers as such has a bearing upon the question of usage of the term "pericycle". The present reviewer has repeatedly advocated abandonment of this term with reference to the peripheral region of the cauline and foliar vascular system of Spermatophyta in which this region is obviously a part of the phloem. No separate region intervenes between the phloem and cortex in such stems, and the leaves associated with them have no pericycle either. The roots, however, usually show a layer or more of tissue outside the vascular elements, a region that may continue to bear the name of "pericycle", at least for the present.

One might object that retention of this term for roots and its abandonment with reference to shoots will destroy the idea of unity of shoot and root. However, the lack of absolute homology of morphologic regions in stem and root is generally recognized. For example, according to Schneider's Handwörterbuch der Botanik (99), the pericycle of root and stem are non-homologous, ontogenetically and physiologically, and therefore the region between the endodermis and the vascular tissues should have different names in the two organs—"pericycle" in the stem, "pericambium" in the root. Recently Allen (2) concluded that, on the basis of histogenesis in embryos of *Pseudotsuga*, "the primary root is homologous with the whole primary shoot having in addition an outer mantle of tissue which has no counterpart in the shoot" and no region exists in "the primary root which can be considered homologous with the cortex of the shoot unless the root pericycle is cortical in nature".

It was stressed in one of the previous reviews (38) that Van Tieghem, in introducing the concept of "pericycle", disregarded the ontogenetic aspect of the problem. Later, however, in his study of the cryptogams (117, 118, 120) he paid attention to ontogeny and decided that *Equisetum* and certain ferns have a double endodermis and no pericycle; that in *Polypodium vulgare* the large steles have a pericycle, the small one has none. Van Tieghem (119) also contended that leaves and astelic stems have no pericycle, because if a stele is absent, so is the "conjunctif", and without the latter there are no pith, no rays and no pericycle. He

proposed the term "peridesme" for the parenchyma between the endodermis and the vascular tissues in astelic organs. In an early paper written before the introduction of the term "pericycle", Van Tieghem (116) reported that, whereas the "rhizogenous membrane" (pericycle) occurred between the vascular tissues and the "protective layer" (endodermis) in the root of a seedling, at higher levels of the latter, where the stem structure appeared, the phloem cells were touching the endodermis. Dangeard (28) and Fischer (49) made similar observations. These examples of Van Tieghem's treatment of the "pericycle" show that even the creator of the term allowed for a certain variability in the fundamental plan of plant structure and could envisage the absence of pericycle.

It is useful to recall also the opinion of Brebner (12)—the investigator whose name is so prominent in the literature dealing with the concept of stele—on the morphologic value of pericycle. He appreciated the advance made by Van Tieghem "in emphasizing the importance of the vascular conducting cylinder as a whole by his stelar terminology" but also felt "that a certain number of the terms did not fit" the views resulting from newer studies. For example, Brebner thought that the histogenetic layers, the endodermis and the pericycle "should be, in many cases, abandoned as morphologic criteria" and that perhaps the phloem should be fixed as the outermost limit of the stele because the "pericycle" is so inconstant in its origin. In fact, according to Brebner (12, p. 548), "it would perhaps have been better to abandon the stelar theory altogether, and substitute for it the conception of a connected system of vascular strands on the one hand and nonvascular on the other. At the same time the nonvascular tissue would not be considered as something essentially and fundamentally different from the vascular for they both are differentiated from the same meristem, and what has become vascular in one case might very well be nonvascular in another and *vice versa*". And finally (12, p. 549), "perhaps the time is hardly yet ripe, but the day does not seem far off when the three histogenetic layers, as well as cortex, pith, endodermis, pericycle, etc., will have lost to a great extent their present morphological connotation and be used simply as convenient descriptive terms in certain cases". Since Brebner wrote this significant statement, the "three histogenetic layers" have lost their morphological connotation, and the

time has become ripe to reexamine thoroughly the concept of "pericycle"; and it seems obvious that the origin of the term "pericycle" and the treatment and critique of it by investigators prominently involved in the evolution of the stelar concept do not support the recently expressed contention (8) that "the background for the term 'pericycle' is much broader than the present bases for negating its existence."

In the delimitation of tissue regions in plant organs, physiologic considerations are perhaps as useful as the ontogenetic. Van Fleet (121–123) has clearly shown, for example, that the characteristics of the limiting layer between the vascular region and the cortex are determined by the reaction of substances originating in the two regions. Thus, although the endodermis of the root may not be homologous with the innermost cortical layer of the stem, physiologically both are analogous; both represent "a boundary between two physiologic systems, the cortex and the stele", where the "effusa from one system may become halted and deposited at the boundary of another" (121).

In the "endodermis" as interpreted by Van Fleet we have a practical topographic as well as functional concept. It enhances our understanding of the inter-relation between tissue regions and gives a concrete basis for regarding the plant body as an organized unit. In contrast, introduction of the term "pericycle" in the purely morphologic sense of Van Tieghem has for many years obscured the understanding of structure and differentiation of the primary phloem and has perpetuated an erroneous idea about the nature of the peripheral part of the vascular system in the higher plants.

To conclude the consideration of the pericycle, a list of families is appended whose representatives (one or more) were found to have the primary phloem in contact with the cortex. Léger (72) contributed the largest number of names to this list: Apocynaceae, Asclepiadaceae, Boraginaceae, Chenopodiaceae, Compositae (Radiatae, Tubuliflorae, Liguliflorae), Cruciferae, Hippocastanaceae, Labiatae, Leguminosae, Lythraceae, Magnoliaceae, Malvaceae, Menispermaceae, Onagraceae, Polygonaceae, Rosaceae, Scrophulariaceae, Solanaceae. To these may be added Linaceae (37), Moraceae (68), Tiliaceae (68) and Vitaceae (44). In the following families Léger (72) was not prepared to deny the presence of

a pericycle because he found a separate tissue region intervening between the phloem and cortex: Caryophyllaceae, Commelinaceae, Cucurbitaceae, Geraniaceae, Liliaceae.

CONCLUSION

The present review may be appropriately terminated with a similar summation of the concept of phloem as the previous review (33) but revised with a view on the investigations of the last decade.

The modern concept of phloem is that of a tissue containing highly specialized cells, the "sieve elements", which together with the parenchymatous members of the phloem form anastomosing strands as a part of the vascular system. The protoplasts of the sieve elements are intimately connected with each other through localized wall portions occupied by "sieve areas" which are comparable to pits in their origin and fundamental structure. The connecting strands in the sieve areas vary greatly in size but are usually more conspicuous than plasmodesmata and are typically associated with variable amounts of callose in the wall region they traverse. The slime which occurs in larger or smaller amounts in sieve-element protoplasts appears to be associated in some obscure manner with the cytoplasm of the connecting strands. In the lower vascular plants and the gymnosperms the sieve elements usually have one type of sieve area on various walls and are called "sieve cells". In angiosperms the sieve areas of certain walls, usually those of the end walls, are particularly well differentiated and form "sieve plates", simple (one sieve area) or compound (two or more sieve areas). The sieve elements of the angiosperms, the "sieve-tube elements", are arranged in longitudinal rows and form thus the "sieve tubes". The protoplasts of the sieve elements lose their nuclei upon maturation and become highly sensitive to mechanical manipulations to which they commonly respond with displacement of contents. The parietal cytoplasm is thin, usually poorly delimited from the vacuole, and of low chromaticity. Although it has been shown to respond with plasmolysis to hypertonic solutions, the cell sap appears to pass readily from element to element through the sieve areas. The parenchyma cells show different degrees of ontogenetic and physiologic relation to the sieve elements. The companion cells of angiosperms are

most closely associated with these elements; then follow the albuminous cells of gymnosperms and finally the phloem parenchyma and ray cells. The sieve elements are relatively short lived. The companion and albuminous cells die at the same time as the sieve elements.

LITERATURE CITED

1. ABBE, L. B. and CRAFTS, A. S. Phloem of white pine and other coniferous species. Bot. Gaz. **100**: 695-722. 1939.
2. ALLEN, G. S. Embryogeny and the development of the apical meristems of *Pseudotsuga*. III. Development of the apical meristems. Am. Jour. Bot. **34**: 204-211. 1947.
3. ARTSCHWAGER, ERNST. Contribution to the morphology and anatomy of guayule (*Parthenium argentatum*). U. S. Dept. Agr., Tech. Bul. 842. 33 p. 1943.
4. ————. Contribution to the morphology and anatomy of *Cryptostegia* (*Cryptostegia grandiflora*). U. S. Dept. Agr., Tech. Bul. 915. 40 p. 1946.
5. AVERY, G. S., JR. Structural responses to the practice of topping tobacco plants: a study of cell size, cell number, leaf size, and veinage of leaves at different levels on the stalk. Bot. Gaz. **96**: 314-329. 1934
6. BAILEY, I. W. and ZIRKLE, CONWAY. The cambium and its derivative tissues. VI. The effects of hydrogen ion concentration in vital staining. Jour. Gen. Physiol. **14**: 363-383. 1931.
7. BARANETZKI, J. Épaississement des parois des éléments parenchymateux. Ann. Sci. Nat., VII, Bot. **4**: 134-201. 1886.

7*a*. BARGHOORN, E. S., JR. Origin and development of the uniseriate ray in the Coniferae. Bull. Torrey Bot. Club **67**: 303-328. 1940.

8. BLASER, H. W. Anatomy of *Cryptostegia grandiflora* with special reference to the latex system. Am. Jour. Bot. **32**: 135-141. 1945.
9. BLIESENICK, HERMANN. Ueber die Obliteration der Siebröhren. Inaug. Diss. Erlangen. 63 p. 1891.
10. BOND, T. E. T. Studies in the vegetative growth and anatomy of the tea plant (*Camellia thea* Link.) with special reference to the phloem. I. The flush shoot. Ann. Bot. **6**: 607-630. 1942.

11*a*. BOUVRAIN, GEORGES. Sur une équivalence du liber précurseur des Gymnospermes chez une Crucifère. Acad. Sci. Paris, Compt. Rend. **211**: 282-285. 1940.

11*b*. ————. Recherches ontogéniques sur les Angiospermes Dicotylédones. 276 p. Diss. Paris. 1941.

12. BREBNER, GEORGE. On the anatomy of *Danaea* and other Marattiaceae. Ann. Bot. **16**: 517-552. 1902.
13. BROWN, H. P. Growth studies in forest trees. 2. *Pinus strobus* L. Bot. Gaz. **59**: 197-241. 1915.
14. CHEADLE, V. I. Observations on the phloem in the Monocotyledoneae. II. Additional data on the occurrence and phylogenetic specialization in structure of the sieve tubes in the metaphloem. Am. Jour. Bot. **35**: 129-131. 1948.
15. ———— and WHITFORD, N. B. Observations on the phloem in the Monocotyledoneae. I. The occurrence and phylogenetic specialization in structure of the sieve tubes in the metaphloem. Am. Jour. Bot. **28**: 623-627. 1941.
16. ———— and UHL, N. W. The relation of metaphloem to the types of vascular bundles in the Monocotyledoneae. Am. Jour. Bot. **35**: 578-583. 1948.

17. CHEN, CHAO-HSI. The development of vascular tissues and the initiation of the inflorescence in *Holcus sorghum*. Iowa State Coll., Jour. Sci. **12**: 217-225. 1938.
18. COMMITTEE ON NOMENCLATURE, INTERNAT. ASSOC. OF WOOD ANATOMISTS. Glossary of terms used in describing woods. Tropical Woods **1933** (36): 1-12. 1933.
19. CRAFTS, A. S. Sieve-tube structure and translocation in the potato. Pl. Physiol. **8**: 81-104. 1933.
20. ———. Translocation in plants. Pl. Physiol. **13**: 791-814. 1938.
21. ———. The relation between structure and function of the phloem. Am. Jour. Bot. **26**: 172-177. 1939.
22. ———. The protoplasmic properties of sieve tubes. Protoplasma **33**: 389-398. 1939.
23. ———. Movement of viruses, auxins and chemical indicators in plants. Bot. Rev. **5**: 471-504. 1939.
24. ———. Vascular differentiation in the shoot apex of *Sequoia sempervirens*. Am. Jour. Bot. **30**: 110-121. 1943.
25. ———. Vascular differentiation in the shoot apices of ten coniferous species. Am. Jour. Bot. **30**: 382-393. 1943.
26. ———. Movement of materials in phloem as influenced by the porous nature of the tissues. *In*: Interaction of water and porous materials. Faraday Soc. Disc. No. 3: 153-159. 1948.
27. CURTIS, O. F. and ASAI, G. N. Evidence relative to the supposed permeability of sieve-tube protoplasm. Am. Jour. Bot. **26**: 16s-17s. 1939. [Abs.]
28. DANGEARD, P. A. Recherches sur le mode d'union de la tige et de la racine chez les Dicotylédones. Botaniste **1**: 75-125. 1889.
29. DIPPEL. Ueber die Zusammensetzung des Gefässbündels der Kryptogamen. Amtl. Ber. Deut. Naturf. und Aerzte. **1864**: 142-148. 1864.
30. EAMES, A. J. and MACDANIELS, L. H. An introduction to plant anatomy. 2nd ed. 427 p. 1947.
31. ENGARD, C. J. Organogenesis in *Rubus*. Univ. Hawaii, Res. Publ. 21. 234 p. 1944.
32. ESAU, KATHERINE. Ontogeny and structure of the phloem of tobacco. Hilgardia **11**: 343-424. 1938.
33. ———. Development and structure of the phloem tissue. Bot. Rev. **5**: 373-432. 1939.
34. ———. Phloem anatomy of tobacco affected with curly top and mosaic. Hilgardia **13**: 437-490. 1941.
35. ———. Vascular differentiation in the vegetative shoot of *Linum*. I. The procambium. Am. Jour. Bot. **29**: 738-747. 1942.
36. ———. Vascular differentiation in the vegetative shoot of *Linum*. II. The first phloem and xylem. Am. Jour. Bot. **30**: 248-255. 1943.
37. ———. Vascular differentiation in the vegetative shoot of *Linum*. III. The origin of the bast fibers. Am. Jour. Bot. **30**: 579-586. 1943.
38. ———. Origin and development of primary vascular tissues in seed plants. Bot. Rev. **9**: 125-206. 1943.
39. ———. Vascular differentiation in the pear root. Hilgardia **15**: 299-324. 1943.
40. ———. Ontogeny of the vascular bundle in *Zea Mays*. Hilgardia **15**: 327-368. 1943.
41. ———. Vascularization of the vegetative shoots of *Helianthus* and *Sambucus*. Am. Jour. Bot. **32**: 18-29. 1945.
42. ———. A study of some sieve-tube inclusions. Am. Jour. Bot. **34**: 224-233. 1947.
43. ———. Some anatomical aspects of plant virus disease problems. II. Bot. Rev. **14**: 413-449. 1948.

44. ————. Phloem structure in the grapevine, and its seasonal changes. Hilgardia **18**: 217-296. 1948.
45. FAULL, A. Elaioplasts in *Iris*: A morphological study. Jour. Arn. Arb. **16**: 225-267. 1935.
46. FINCH, A. H. Notes on the physiology of apple varieties. Am. Soc. Hort. Sci., Proc. **24**: 212-216. 1927.
47. ————. Physiology of apple varieties. Pl. Physiol. **10**: 49-72. 1935.
48. FISCHER, ALFRED. Neue Beiträge zur Kenntnis der Siebröhren. Ber. Verh. Kön. Sächs. Ges. Wiss. Leipzig, Math. Phys. Cl. **38**: 291-336. 1886.
49. FISCHER, HERMANN. Der Pericycel in den freien Stengelorganen. Jahrb. Wiss. Bot. **35**: 1-27. 1900.
50. FOSTER, A. S. Practical plant anatomy. 155 p. 1942.
51. FRITSCH, F. E. The structure and reproduction of the algae. Vol. II. 939 p. 1945.
52. GHOSH, S. S., *et al.* Anatomical studies on jute (*Corchorus*) with special reference to the formation of fibre. Indian Centr. Jute Comm. Agr. Res. Mem. 1. 24 p. 1943.
53. GILL, N. The phloem of ash (*Fraxinus excelsior* Linn.), its differentiation and seasonal variation. Leeds Phil. Soc. Proc. **2**: 347-355. 1932.
54. ————. The relation of flowering and cambial activity. Observations on vascular differentiation and dry-weight changes in the catkins of some early flowering catkin-bearing dicotyledons. New Phytol. **32**: 1-12. 1933.
54a. GOLUB, S. J. and WETMORE, R. H. Studies of the development in the vegetative shoot of *Equisetum arvense* L. II. The mature shoot. Am. Jour. Bot. **35**: 767-781. 1948.
55. GUILLIERMOND, ALEXANDRE. The cytoplasm of the plant cell. 247 p. 1941.
56. GUNKEL, J. E. and WETMORE, R. H. Studies of development in long shoots and short shoots of *Ginkgo biloba* L. II. Phyllotaxis and the organization of the primary vascular system; primary phloem and primary xylem. Am. Jour. Bot. **33**: 532-543. 1946.
57. HANSTEIN, JOHANNES. Die Milchsaftgefässe und die verwandten Organe der Rinde. 92 p. 1864.
58. HARTIG, THEODOR. Vergleichende Untersuchungen über die Organisation des Stammes der einheimischen Waldbäume. Jahresb. Fortschr. Forstwiss. und Forstl. Naturkunde **1**: 125-168. 1837.
59. ————. Ueber die Querscheidewände zwischen den einzelnen Gliedern der Siebröhren in *Cucurbita Pepo*. Bot. Zeit. **12**: 51-54. 1854.
60. HEMENWAY, A. F. Studies on the phloem of the dicotyledons. I. Phloem of the Juglandaceae. Bot. Gaz. **51**: 131-135. 1911.
61. ————. Studies on the phloem of the dicotyledons. II. The evolution of the sieve-tube. Bot. Gaz. **55**: 236-243. 1913.
62. HUBER, BRUNO. Das Siebröhrensystem unserer Bäume und seine jahreszeitlichen Veränderungen. Jahrb. Wiss. Bot. **88**: 176-242. 1939.
63. ————. Gesichertes und Problematisches in der Wanderung der Assimilate. Ber. Deut. Bot. Ges. **59**: 181-194. 1941.
64. ————. Die Siebröhren der Pflanzen als Nahrungsquelle fremder Organismen und als Transportbahnen von Krankheitskeimen. Biol. Gen. **16**: 310-343. 1942.
65. ———— and ROUSCHAL, ERNST. Anatomische und zellphysiologische Beobachtungen am Siebröhrensystem der Bäume. Ber. Deut. Bot. Ges. **56**: 380-391. 1938.

66. ————, *et al.* Untersuchungen über den Assimilatstrom. I. Tharandter Forstl. Jahrb. **88:** 1017-1050. 1937.
67. KNUDSON, L. Observations on the inception, season and duration of the cambium development in the American larch (*Larix laricina* (du Roi) Koch.) Bul. Torrey Bot. Club **40:** 271-293. 1913.
68. KUNDU, B. C. The anatomy of two Indian fibre plants, *Cannabis* and *Corchorus* with special reference to fibre distribution and development. Jour. Indian Bot. Soc. **21:** 93-128. 1942.
69. ————. Anatomy of jute stem with special reference to cambial activity and distribution of fibres in relation to leaf-trace system. Jour. Royal Asiatic Soc. Bengal. Science **10:** 27-52. 1944.
70. KÜSTER, ERNST. Die Pflanzenzelle. 672 p. 1935.
71. LECOMTE, H. Contribution à l'étude du liber des Angiospermes. Ann. Sci. Nat., **10** Bot.: 193-324. 1889.
72. LÉGER, L. J. Recherches sur l'origine et les transformations des éléments libériens. Soc. Linn. Normandie, Mém. **19:** 49-182. 1897.
73. LENOIR, MAURICE. La télophase de la division I dans le sac embryonnaire du *Fritillaria imperialis* L. Acad. Sci. Paris, Compt. Rend. **180:** 160-163. 1925.
74. MACDANIELS, L. H. The histology of the phloem in certain woody angiosperms. Am. Jour. Bot. **5:** 347-378. 1918.
75. MANGENOT, G. Communications intercellulaires et synapses. Notes d'histologie végétale. Bul. d'Histol. Appl. à la Physiol. et Path. et de Tech. Micros. **3:** 142-160. 1926.
76. MARTENS, P. and PIGNEUR, H. Les espaces intercellulaires du tissue criblé. Cellule **51:** 185-192. 1947.
77. MASON, T. G. Preliminary note on the physiological aspects of certain undescribed structures in the phloem of the greater yam, *Dioscorea alata* Linn. Royal Dublin Soc., Sci. Proc. **18:** 195-198. 1926.
78. ———— and PHILLIS, E. The migration of solutes. Bot. Rev. **3:** 47-71. 1937.
79. MAUGINI, ELENA. Alcune osservazioni sul contenuto del cribro in giovani fusti di "Guizotia Abyssinica" Cass. Nuovo Gior. Bot. Ital. **50:** 75-78. 1943.
80. MEYER, ARTHUR. Das Chlorophyllkorn in chemischer, morphologischer und biologischer Beziehung. 91 p. 1883.
81. MILANEZ, F. R. Nota prévia sôbre os laticíferos de *Hevea brasiliensis.* Arqu. do Serv. Florestal **2:** 39-65. 1946.
82. MILLER, H. A. and WETMORE, R. H. Studies in the developmental anatomy of *Phlox Drummondii* Hook. III. The apices of the mature plant. Am. Jour. Bot. **33:** 1-10. 1946.
83. MOELLER, JOSEPH. Anatomie der Baumrinden. 447 p. 1882.
84. MÜNCH, ERNST. Die Stoffbewegungen in der Pflanze. 234 p. 1930.
85. ————. Durchlässigkeit der Siebröhren für Druckströmungen. Flora **36:** 223-262. 1943.
86. PIGNEUR, HECTOR. L'ontogenese du tube criblé chez *Cucurbita* et *Athurium.* Cellule **51:** 259-278. 1947.
86*a*. PLYMALE, E. L. and WYLIE, R. B. The major veins of mesomorphic leaves. Am. Jour. Bot. **31:** 99-106. 1944.
87. PRIESTLEY, J. H. Radial growth and extension growth in the tree. Forestry **9:** 84-95. 1935.
88. RAATZ, WILHELM. Die Stabbildungen im secundären Holzkörper der Bäume und die Initialtheorie. Jahrb. Wiss. Bot. **23:** 567-636. 1892.
89. REEVE, R. M. Structure and growth of the vegetative shoot apex of *Garrya elliptica* Dougl. Am. Jour. Bot. **29:** 697-711. 1942.
90. ROBERTS, R. H. and WILTON, O. C. Phloem development and blossoming. Science **84:** 391-392. 1936.

91. Roecki, Brunhild. Nachweis eines Konzentrationshubs zwischen Palisadenzellen und Siebröhren. Inaug. Diss. München, 1948. [Unpublished.]
92. Rouschal, Ernst. Untersuchungen über die Protoplasmatik und Funktion der Siebröhren. Flora **35**: 135-200. 1941.
93. Russow, Edmund. Vergleichende Untersuchungen betreffend die Histologie der vegetativen und sporenbildenden Organe und die Entwickelung der Sporen der Leitbündel-Kryptogamen, mit Berücksichtigung der Histologie der Phanerogamen, ausgehend von der Betrachtung der Marsiliaceen. Acad. Imp. Sci. St. Petersburg, Mém., VII, **19**: 1-207. 1872.
94. ————. Betrachtungen über das Leitbündel und Grundgewebe aus vergleichend morphologischem und phylogenetischem Gesichtspunkt. 78 p. 1875.
95. Salmon, Janine. Différenciation des tubes criblés chez les Angiospermes. Recherches cytologiques. 235 p. Copyright 1947 by J. Salmon. 1946. [Also, in somewhat abbreviated form, in Rev. de Cytol. et de Cytophysiol. Vég. **9**: 55-168. 1946-47.]
96. Scarth, G. W. The mechanism of accumulation of dyes in living cells. Pl. Physiol. **1**: 215-229. 1926.
97. Schaede, Reinhold. Ueber den Feinbau der Parenchymmembranen. Ber. Deut. Bot. Ges. **58**: 275-290. 1940.
98. Schmidt, E. W. Bau und Funktion der Siebröhre der Angiospermen. 108 p. 1917.
99. Schneider, C. K. Illustriertes Handwörterbuch der Botanik. 12th ed. 824 p. 1917.
100. Schneider, Henry. The anatomy of peach and cherry phloem. Bul. Torrey Bot. Club **72**: 137-156. 1945.
101. Schumacher, Anneliese. Beitrag zur Kenntnis des Stofftransportes in dem Siebröhrensystem höherer Pflanzen. Planta **35**: 642-700. 1948.
102. Schumacher, Walter. Untersuchungen über die Lokalisation der Stoffwanderung in den Leitbündeln höherer Pflanzen. Jahrb. Wiss. Bot. **73**: 770-823. 1930.
103. ————. Untersuchungen über die Wanderung des Fluoreszeins in den Siebröhren. Jahrb. Wiss. Bot. **77**: 685-732. 1933.
104. ————. Weitere Untersuchungen über die Wanderung von Farbstoffen in den Siebröhren. Jahrb. Wiss. Bot. **85**: 422-449. 1937.
105. ————. Ueber die Plasmolysierbarkeit der Siebröhren. Jahrb. Wiss. Bot. **88**: 545-553. 1939.
106. Sharman, B. C. Developmental anatomy of the shoot of *Zea mays* L. Ann. Bot. **6**: 245-282. 1942.
107. Shimakura, Misaburô. On the expansion of bast cells in conifers. Bot. Mag. Tokio **50**: 318-323. 1936.
108. Small, J. Technique for the observation of protoplasmic streaming in sieve tubes. New Phytol. **38**: 176-177. 1939.
109. Smith, A. I. The comparative histology of some of the Laminariales. Am. Jour. Bot. **26**: 571-585. 1939.
110. Sterling, Clarence. Growth and vascular development in the shoot apex of *Sequoia sempervirens* (Lamb.) Endl. III. Cytological aspects of vascularization. Am. Jour. Bot. **33**: 35-45. 1946.
111. ————. Organization of the shoot of *Pseudotsuga taxifolia* (Lamb.) Britt. II. Vascularization. Am. Jour. Bot. **34**: 272-280. 1947.
112. Struckmeyer, B. E. Structure of stems in relation to differentiation and abortion of blossom buds. Bot. Gaz. **103**: 182-191. 1941.
113. ———— and Roberts, R. H. Phloem development and flowering. Bot. Gaz. **100**: 600-606. 1939.

114. ———— and ————. Effect of photoperiod and temperature upon the growth of seedlings and cuttings. Am. Jour. Bot. **26**: 694-697. 1939.
115. ———— and ————. Investigations on the time of blossom induction in Wealthy apple trees. Am. Soc. Hort. Sci., Proc. **40**: 113-119. 1942.
116. TIEGHEM, PH. VAN. Mémoire sur les canaux sécréteurs des plantes. Ann. Sci. Nat., V., Bot. **16**: 96-201. 1872.
117. ————. Sur la limite du cylindre central et de l'écorce dans les Cryptogames vasculaires. Jour. de Bot. **2**: 369-377. 1888.
118. ————. Sur le dédoublement de l'endoderme dans les Cryptogames vasculaires. Jour. de Bot. **2**: 404-406. 1888.
119. ————. Péricycle et péridesme. Jour. de Bot. **4**: 433-435. 1890.
120. ————. Traité de botanique. 2nd ed. 2 vols. 1855 p. 1891.
121. VAN FLEET, D. S. The development and distribution of the endodermis and an associated oxidase system in monocotyledonous plants. Am. Jour. Bot. **29**: 1-15. 1942.
122. ————. The significance of oxidation in the endodermis. Am. Jour. Bot. **29**: 747-755. 1942.
123. ————. The enzymatic and vitagen properties of unsaturated fats as they influence the differentiation of certain plant tissues. Am. Jour. Bot. **30**: 678-685. 1943.
124. WEST, CYRIL and TAKEDA, H. On *Isoetes japonico*. Linn. Soc. London, Trans. Bot. **8**: 333-369. 1913.
125. WILHELM, KARL. Beiträge zur Kenntnis des Siebröhrenapparates dicotyler Pflanzen. 90 p. 1880.
126. WILLIAMS, B. C. The structure of the meristematic root tip and origin of primary tissues in the roots of vascular plants. Am. Jour. Bot. **34**: 455-462. 1947.
127. WILSON, C. L. Lignification of mature phloem in herbaceous types. Am. Jour. Bot. **9**: 239-244. 1922.
128. WILTON, O. C. Correlation of cambial activity with flowering and regeneration. Bot. Gaz. **99**: 854-864. 1938.
129. ———— and ROBERTS, R. H. Anatomical structure of stems in relation to the production of flowers. Bot. Gaz. **98**: 45-64. 1936.
130. ZIRKLE, CONWAY. The plant vacuole. Bot. Rev. **3**: 1-30. 1937.

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